Landscape and Urban Planning 89 (2009) 28–36

Contents lists available at ScienceDirect

Landscape and Urban Planning

journal homepage: www.elsevier.com/locate/landurbplan

Modeling urban land development as a continuum to address fine-grained habitat heterogeneity

Patricia N. Manley[a,*], Sean A. Parks[a,1], Lori A. Campbell[a], Matthew D. Schlesinger[a,b,2]

[a] USDA Forest Service, Pacific Southwest Research Station, Sierra Nevada Research Center, 1731 Research Park Drive, Davis, CA 95618, USA
[b] Department of Environmental Science and Policy and Graduate Group in Ecology, University of California, One Shields Avenue, Davis, CA 95616, USA

ARTICLE INFO

Article history:
Received 30 July 2007
Received in revised form 11 June 2008
Accepted 16 September 2008
Available online 25 November 2008

Keywords:
Landscape analysis
Biodiversity conservation
Lake Tahoe
California spotted owl
Montane forest
Urbanization

ABSTRACT

Natural landscapes are increasingly subjected to impacts associated with urbanization, resulting in loss and degradation of native ecosystems and biodiversity. Traditional classification approaches to the characterization of urbanization may prove inadequate in some human-modified landscapes where complex and unique combinations of conditions can make classification and delineation of patches difficult. We describe a model that depicts existing human development as a fine-grained continuous variable using parcel-based land use data and transportation networks. We derived percent development values across our 88 000-ha study area, the Lake Tahoe basin. Our modeled values were highly correlated with observed levels of development based on high-resolution aerial photographs. We demonstrate how our model of development can be used to address practical conservation questions by evaluating the potential effects of highly interspersed urban land development and wildland conditions on the amount and availability of habitat suitable for the resident California spotted owl (*Strix occidentalis occidentalis*) at two points in time (current and 40 years in the future). The results indicated that assessments not accounting for the indirect effects of development may overestimate the amount of available habitat by 19–83%. Portraying urbanization as a continuum across entire landscapes captured fine-grained landscape complexity at scales that were relevant to the habitat needs and environmental sensitivities of a species of conservation interest. This relatively simple approach should aid ecologists and landscape planners in evaluating the current or future effects of urbanization on ecological elements and processes.

Published by Elsevier B.V.

1. Introduction

The pattern, pace, and character of urban growth can all substantially affect the ecological integrity and function of landscapes (Turner, 1989; McDonnell and Pickett, 1990; Marzluff and Ewing, 2001; Luck and Wu, 2002). Urbanization is an increasingly prevalent cause of species endangerment and alteration of ecological communities (McKinney, 2002, 2006), and thereby calls for the development of incisive and readily available tools for studying its effects on habitat conditions at a range of spatial and temporal scales. As our understanding of urban ecosystems progresses, so does the potential to retain more elements and functions of native ecosystems as an integral part of the urbanizing landscape through thoughtful assessment and informed planning. The ability of researchers, managers, and planners to more readily and critically assess the consequences of alternative development scenarios will improve the potential of landscapes to support native biological diversity while meeting the needs of a growing human population (Turner et al., 2001).

Landscape-assessment tools that facilitate simultaneous evaluation of varied ecosystem properties at their appropriate spatial scales, including habitat conditions for multiple animal and plant species, are needed to improve the analytic capacity of urban planning (e.g., Sandström et al., 2006; Cadenasso et al., 2007). When urban development is highly intertwined with wildlands, habitat occupancy and quality (i.e., reproductive success) are likely to be affected not only by habitat structure and configuration, but also by disturbance, such as presence of humans, domestic animals, and vehicle traffic (Boyle and Samson, 1985; Churcher and Lawton, 1987; Knight and Gutzwiller, 1995; Forman et al., 2002; Blumstein et al., 2005). Thus, landscape-assessment tools must be able to account for a variety of direct and indirect effects of urbanization that may be expressed at a range of scales from coarse-grained configurations across large watersheds to fine-grained interfaces of

* Corresponding author. Tel.: +1 530 759 1719; fax: +1 530 747 0241.
E-mail address: pmanley@fs.fed.us (P.N. Manley).
[1] Present address: USDA Forest Service, Aldo Leopold Wilderness Research Institute, Rocky Mountain Research Station, 790 East Beckwith Avenue, Missoula, MT 59801, USA.
[2] Present address: New York Natural Heritage Program, 625 Broadway, 5th Floor, Albany, NY 12233-4757, USA.

0169-2046/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.landurbplan.2008.09.005

urban and wildland elements at the scale of backyards and neighborhoods.

In response to the unique challenge of characterizing landscapes in urbanizing areas, researchers have gravitated toward recognizing urban land development as a gradient of conditions (McDonnell and Pickett, 1990; Marzluff et al., 2001; Theobald, 2004). Portraying urban development as a continuum has the ability to reveal thresholds of biological and ecological responses to human-induced stress more precisely (Alberti et al., 2001; Theobald, 2004). For instance, broad categories of population density available from the U.S. Census Bureau have been used as a proxy for urbanization intensity, but these data portray uniform population densities across large areas and therefore are weak in their ability to account for fine-grained heterogeneity in developed areas. Further, commercial areas (e.g., shopping centers, golf courses) and public service areas (e.g., schools, airports, ballparks) are not portrayed as urban even though they are human-dominated land uses. Distance from an urban core also has been used as a measure of urbanization intensity, but it assumes a uniform decrease in development intensity in all directions, which is often not the case (Alberti et al., 2001).

The impervious-surface data layer available in the National Land Cover Database (NLCD) for the conterminous United States (Homer et al., 2007) has great potential for portraying urbanization as a gradient, but at the present time it carries some important limitations. Although the 30 m × 30 m grid cells are attributed with percent impervious values, they do not represent urban land uses that are pervious, such as golf courses, lawns, dirt roads, etc. Furthermore, the NLCD impervious layer restricts impervious cells to an urban mask, which excludes impervious cells that may be outside or on the fringes of the designated urban mask, and its overall accuracy remains unquantified.

Land-use classifications available from digital county parcel maps offer a valuable alternative to the limitations present in other publicly available data sources (e.g., Wickham and Norton, 1994; Wear et al., 1998; Brown and Vivas, 2005). Although their use so far has been limited to the classification of areas ranging from individual parcels to larger regions, they have the potential to represent urbanization as a gradient at a scale that can reflect fine-grained heterogeneity. In this paper we describe the creation of a continuous development surface based on land-use classification and illustrate how it can be used to evaluate the potential effects of development on habitat conditions for a forest-associated species in a landscape with a fine-grained interspersion of wildland and urban ecosystems.

We had the following objectives: (1) create a fine-grained continuous surface of urbanization to facilitate interpretations of habitat conditions at multiple spatial scales; and (2) assess the ability of the model to address the potential effects of current and future landscape alteration on suitability and availability of habitat for the California spotted owl (*Strix occidentalis occidentalis*), a forest-associated species of conservation interest.

2. Methods

2.1. Study area

Our study area was the Lake Tahoe basin (Fig. 1), where there is a high level of interface between development and native vegetation, particularly at lower elevations in proximity to Lake Tahoe. The 88 000-ha Lake Tahoe basin lies in the central Sierra Nevada, with its western half in California and its eastern half in Nevada. The basin spans nearly 1500 m of elevation and three life zones: the lower montane, dominated by Jeffrey pine (*Pinus jeffreyii*) and white fir (*Abies concolor*); the upper montane, dominated by mixed conifer; and the subalpine, dominated by red fir (*Abies magnifica*) (Manley et al., 2000). The basin is well known for its natural beauty, but the terrestrial environment and the lake itself have been degraded over the past 100 years, with urban development being a primary source of impacts (Manley et al., 2000).

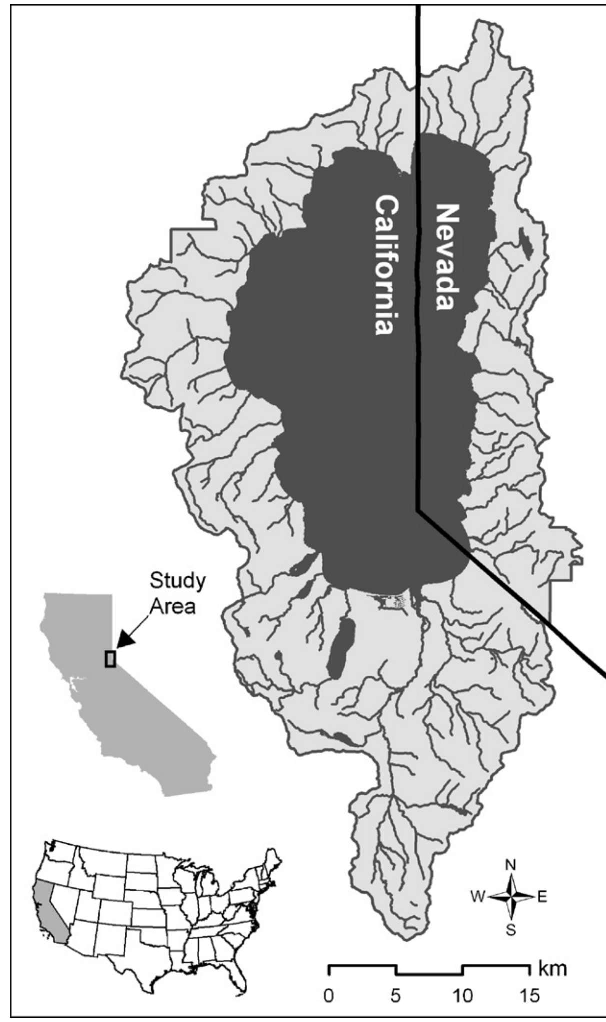

Fig. 1. Location of the Lake Tahoe basin study area.

Much of the landscape is occupied by native vegetation and most (approximately 75%) of the Lake Tahoe basin is in public ownership. While there are remnant forests within urbanized areas of the basin, the overall pattern of development does not conform to the patch-matrix pattern seen commonly with forest clearing for agriculture or high-intensity development. Rather, the basin retains much of the original vegetation within developed areas. Local building regulations require that a set proportion of each land parcel remain in permeable condition and retain native trees. In residential areas, for instance, pine trees and other native vegetation commonly occur in yards and between houses. Commercial areas are concentrated near the lake and include high-intensity developments such as shopping centers and large hotels and casinos. Recreation-related developments, such as mountain bike trails, campgrounds, and golf courses occur throughout the basin in response to the approximately three million visitors per year (Nechodom et al., 2000; Kosis et al., 2002).

2.2. Urban model development

We modeled the pattern of development in the basin using three digital data types: a parcel-based land-use layer, transportation layers, and digital orthophoto quarter quads (DOQQs; basically digital aerial photographs). These digital data are available in many urbanizing areas in the U.S.; therefore, methods used here or correlates thereof could be replicated elsewhere. We defined as "developed" any land use that entailed removal of native vegetation; for example, housing developments and golf courses are development, whereas snow ski runs are not development.

We assigned levels of development to each land-use type as defined and identified in the Lake Tahoe basin parcel map created by the Tahoe Regional Planning Agency (2001). Each of the 60 137 land parcels within the basin was assigned one of 90 land-use types, such as single-family dwelling, hotel/motel, service station, and animal husbandry services (Appendix A). About 3% of the parcels did not have a county-assigned land-use type, and for these we consulted DOQQs and used personal knowledge of the basin to assign one of the standard land-use types. Public lands in the basin are generally undeveloped, but they contain many miles of paved and dirt roads. Therefore, we augmented the parcel layer with transportation layers developed by the USDA Forest Service (Cahill et al., 2002) and the states of California and Nevada (California State Parks circa, 2000; Nevada Division of State Parks circa, 2000). We estimated the average percent development (not including roads) per parcel associated with each of the 90 land-use types based on a sample of parcels of each land-use type. Roads were quantified separately, since they primarily occur between parcels and their density is not necessarily a function of land-use type. We randomly selected a ≥20% sample of parcels in each land-use type for all but the 20 most abundant land-use types (20 parcels for the 10 types with 51–200 parcels; and 30 parcels for the 10 types with >200 parcels). We estimated the proportion of each parcel that was developed to the nearest 10% using DOQQs from 1998, and then averaged these estimates.

We created a continuous layer of development by estimating the proportion of each 30 m × 30 m sample unit in the Lake Tahoe basin that was occupied by development. We chose a 30-m sample unit as the primary scale of analysis because it was small enough to represent the fine-grained heterogeneity of development in the basin, and it was consistent with the pixel size of many public-domain GIS-data layers (e.g., elevation, satellite thematic mapper data). The development layer was a composite of land-use data and road and trail network data. We created a land-use grid that was composed of 3 m × 3 m pixels that nested within 30-m sample units (100 pixels per sample unit). For each parcel, we randomly selected the appropriate number of 3-m pixels to represent the average development for that land-use type and labeled them as developed.

We created a road and trail grid in a similar manner. We converted the linear road and trail features to areas by buffering each feature to represent its average width: highways, 13.8 m; paved surface streets, 10.2 m; dirt roads, 6.6 m; and trails, 1 m. Buffer widths for paved roads were based on the number of lanes, the standard width of a traffic lane, and the average width of a shoulder (California Department of Transportation, 2001). We overlaid a 3-m grid on the road and trail network and labeled as developed all pixels overlapping a transportation feature. Finally, we combined the land-use and road-trail grids to create a single 3-m pixel development layer (Fig. 2A). We then scaled up to 30-m sample units with percent development values based on the number of developed 3-m pixels occurring within (Fig. 2B).

We also derived an estimate of urban development 40 years in the future for the purpose of providing a context for assessing relative magnitudes of change associated with growth vs. modeling assumptions. We assumed that a portion of currently undeveloped parcels would be developed and that existing development would expand to a limited degree. We used the 2004 rate of building permit issuances (approximately 80 per year), based on the general trend of increasing permitting rates from 1995 to 2001, at which point permitting levels appeared to vary around a mean value of 80 per year (Tahoe Regional Planning Agency, personal communication). Based on this rate, we determined that at least half of the remaining 6500 undeveloped private parcels could be developed in the next 40 years. Assuming that primarily single-family residences would be built on these parcels, we randomly selected half of the undeveloped private parcels and increased their development value to 51%, the average value for single-family residences (Appendix A). We also added a small increment of development (5%) to all developed parcels with commercial, residential or tourist land uses to reflect the high annual volume of permit requests for additions or modifications (e.g., decks, sheds, expansions) received by the Tahoe Regional Planning Agency (Weigel, personal communication).

2.3. Urban model validation

We conducted an evaluation of the accuracy of the development model using 1:15 840-scale color aerial photographs from the year 2000. We randomly selected 116, 30-m sample units, stratified by development level (20% intervals) and basin orientation (N, E, S, W), from the lower elevations (<2120 m), where the greatest range of percent development occurred. We placed a dot grid with a density of approximately one dot per sample unit (11.2 dots/ha) over the photos and centered on the selected sample unit, and counted the number of dots that overlapped development within 300 m (28.3 ha) of the point. We chose a 300-m radius because it encompasses the breadth of sampling areas associated with most of the commonly used biological survey methods for plants and animals in our area (Ralph et al., 1993; Heyer et al., 1994; Zielinski and Kucera, 1995; Wilson et al., 1996; Manley et al., 2006). We used simple linear regression (SAS Institute Inc., 2000) to compare the observed proportion of dots overlapping development to the development model value.

2.4. Habitat assessment example

We demonstrated the importance of accounting for fine-grained heterogeneity and the ability of our development model to do so in an evaluation of the potential effects of urbanization on the availability of suitable habitat of the California spotted owl, a forest-associated species of conservation interest in the Lake Tahoe basin (Manley et al., 2000) and throughout the Sierra Nevada (Verner et al., 1992). We calculated the degree to which evaluations based on structural habitat conditions alone may lead to an overestimate of the extent to which habitat can support the California spotted owl at two scales (nest stands and territories) when development is not considered. Specifically, we compared the potential for the landscape to support breeding owl pairs with and without the consideration of fine-scale development interspersed within suitable habitat. We used existing data on species occurrences in the basin, local research results, state wildlife databases, and published literature to establish parameter values for the evaluation.

We defined suitable habitat by consulting the California Wildlife Habitat Relationships (CWHR) database (Mayer and Laudenslayer, 1988; California Department of Fish and Game, 2002) and published literature (Laymon, 1988; Hunsaker et al., 2002) (Table 1). The CWHR database specifies, for each species, the vegetation types and their tree-diameter and canopy-closure conditions that provide habitat suitable for foraging, nesting, and cover. For nest stands, two minimum tree-diameter and canopy-closure combinations were considered suitable to support reproduction, and for territories, one minimum tree-diameter and canopy-closure condition defined suitable habitat. The dominant forested vegetation types in the

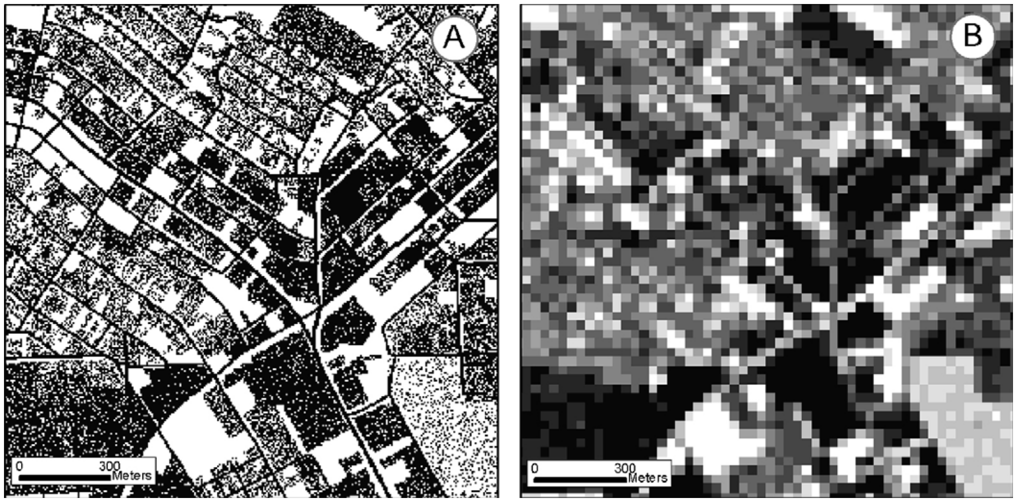

Fig. 2. Modeled development in the Lake Tahoe basin based on land-use type and transportation features at two stages of creation: (A) random allocation of development to 3-m pixels within each parcel based on land use classification; (B) classification of 30 m × 30 m sample units by percent development. Solid white indicates areas with zero development; darker shades of indicate increasing levels of human development.

basin, together comprising 60% of the forested landscape, are Sierran mixed conifer and Jeffrey pine. Two additional vegetation types, lodgepole pine and red fir, comprise another 30% of the forested landscape. The remaining 10% of the forested landscape is occupied by small amounts of seven additional forest types, of which only subalpine conifer and montane riparian exceed 1%. Given the similar suitability of the dominant forest types, we assumed for the purposes of modeling that all forested types that met the tree-diameter and canopy-closure thresholds provided suitable habitat for the California spotted owl. Our characterization of suitable habitat was not intended to be definitive; it was simply a coarse approximation for the purposes of demonstrating the potential applications of our development model to assess a species' habitat needs at multiple spatial scales. We based our evaluation of habitat conditions on the vegetation data layer developed by Dobrowski et al. (2005) from IKONOS satellite imagery, including the minimum tree-diameter and canopy-closure requirements.

We determined the appropriate nest-stand extent and minimum suitable habitat requirements based on published literature and management direction. Nest stands (activity centers around nest sites) ranged from 118.4 to 124.0 ha in the southern Sierra Nevada and averaged 315 ha in the northern Sierra Nevada (Gutierrez et al., 1992). We selected an intermediate nest-stand area of 200 ha. Hunsaker et al. (2002) recommended that nest stands consist of a minimum of 60% high-quality suitable habitat

Table 1
Definition of suitable habitat and minimum amount of habitat required for nest stands (reproduction habitat) and territories (foraging habitat) for the California spotted owl (*Strix occidentalis occidentalis*), based on CWHR database (CDFG, 2002) suitability ratings for reproduction and foraging and recommendations in USDA Forest Service (2004), Call (1990) and Hunsaker et al. (2002).

	Suitable habitat	
	Condition	Amount
Nest stand	Canopy cover ≥ 60% and average dbh* ≥ 28 cm or Canopy cover ≥ 40% and average dbh ≥ 61 cm	≥ 60% of 200 ha
Territory	Canopy cover ≥ 40% and average dbh ≥ 28 cm	≥ 40% of 1000 ha

*Diameter at breast height.

(i.e., large-diameter trees and high canopy cover) and USDA Forest Service (2004) management direction specified that 121 ha of suitable habitat be maintained in nest stands. Consistent with these recommendations, we selected sample units with a minimum of 120 ha of suitable habitat within the surrounding 200-ha nest stand (Table 1).

We determined the appropriate territory extent and minimum habitat requirements based on two research study sites located within 200 km of the Lake Tahoe basin, within which territories averaged 855.5 ha (Laymon, 1988) and 1269.5 ha (Call, 1990). We selected an intermediate territory area of 1000 ha for our assessment. USDA Forest Service (2004) management direction specified a minimum of 400 ha of suitable habitat be maintained within 2.4 km of known nest sites. Consistent with this recommendation, we selected sample units with a minimum of 400 ha of suitable habitat within the surrounding 1000-ha territory (Table 1).

We considered the potential existence of thresholds of tolerance for development rendering all the habitat within a potential nest stand or territory unavailable (e.g., Gutierrez et al., 1992). We used the maximum observed development within nest-stand and territory extents around the seven known occupied nest sites of the California spotted owl in the Lake Tahoe basin as the basis for potential threshold values. At the nest-stand scale, the mean observed development was 2.3% (S.D. = 3.02), so we selected 5% as the threshold (mean plus one standard deviation). Using a similar approach for the territory scale, the mean observed development was 4.2% (S.D. = 4.48), so we selected 10% as the threshold.

We also considered the potential existence of a threshold of tolerance for development occurring within suitable habitat. We applied a low tolerance threshold of <1% developed, meaning that any suitable habitat within a 30-m sample unit containing ≥1% development was considered unavailable. We used this threshold to evaluate potential losses in habitat availability based on development intrusions.

We conducted a moving-window analysis (neighborhood statistics) using ArcMap 9.0 (ESRI Inc., 2004) to evaluate the potential effects of the development thresholds on the proportion of the landscape suitable for territory establishment and nesting. The 30-m sample units were used as the center of moving windows; units that satisfied the evaluation criteria were assigned a value of 1, and otherwise were assigned a value of 0. We evaluated nest-stand conditions within a 200-ha window and territory conditions within a

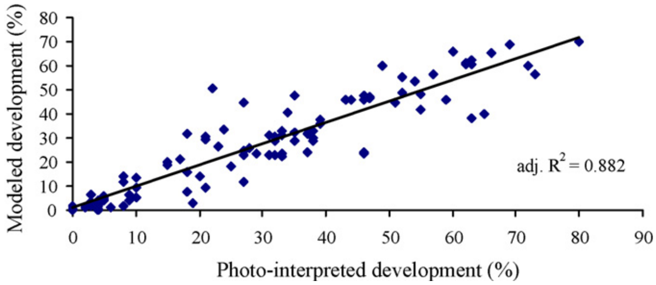

Fig. 3. Correspondence between the modeled development values and values derived from interpretation of aerial photographs. The sets of values represent development within 300 m of 116 points around the Lake Tahoe basin.

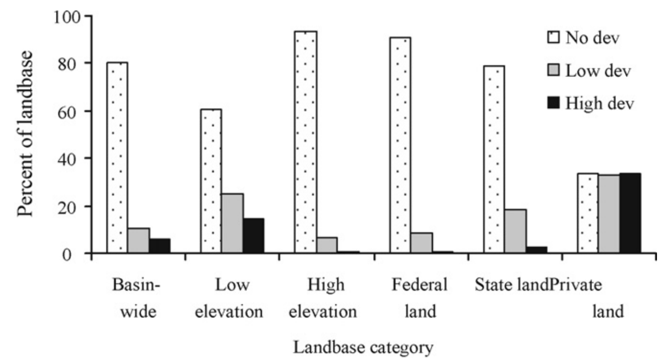

Fig. 4. Percent of area in urban development by elevation (≤ and >2120 m) and land ownership in the Lake Tahoe basin.

1000-ha window (Table 1). We evaluated four habitat availability scenarios for current and potential future urbanized landscapes to determine the relative impact of varying types and levels of development on the potential availability of suitable habitat. For each scenario, we summarized the proportion of the sample units in the basin that satisfied the evaluation criteria.

(1) Considered all suitable habitat grid cells present within the window as available regardless of the amount and location of development.
(2) Considered all suitable habitat grid cells as available regardless of intrusions of development, but imposed a maximum amount of development allowable within the window as a representation of a nest- or territory-scale disturbance threshold (5% and 10%, respectively).
(3) Excluded suitable habitat grid cells that had intrusions of ≥1% development, representing the potential that suitable habitat with fine-grained intrusions of development may not be available for use because of associated human disturbance, but did not impose nest- or territory-scale disturbance threshold.
(4) Excluded suitable habitat grid cells with ≥1% development and applied the development threshold at nest and territory scales (the most restrictive scenario).

3. Results

3.1. Urban model validation

The average percent of the area developed ranged from a low of 14% for summer homes (cabins) to a high of 100% for several land uses, including airfields, marinas and condominiums. The most prevalent land use was single-family dwellings, which had an intermediate level (51%) of development (Appendix A).

The development model values were significantly correlated with the aerial photo-based estimates of development ($r^2 = 0.88$, $F_{1,114} = 863.3$, $P < 0.001$; Fig. 3). The tight fit of the regression line and slope of 0.99 (S.E. = 0.034) indicated that the model closely corresponded to development as it was represented on aerial photographs.

3.2. Urban development patterns

At the time of our analysis, the Lake Tahoe basin was largely undeveloped, with 80% of 30-m sample units within the basin having no (<1%) urban development and only 6% of sample units with high (>50%) development values (Fig. 4). Most of the development was concentrated along the northern, northwestern, and southern slopes of the Lake Tahoe basin at lower elevations in proximity to the lake (Fig. 4). At lower elevations (≤2120 m), 60% of sample units had no development and 15% of sample units had high development; conversely, at higher elevations (>2120 m), 94% of sample units had no development and no units had high development. Development levels also varied among ownerships (Fig. 4). On federal lands, 91% of sample units had zero development and only 1% of sample units had high development. Similarly, nearly 80% of state lands had zero development values and <3% had high development. In contrast, one third of private lands had high development, with equivalent proportions having no and low development. Based on our simple growth parameters, we estimated that 934 ha of native vegetation (1.21% of the basin) could be lost to development in the next 40 years.

3.3. Habitat assessment example

Based on vegetation alone, 41.1% of the grid cells (33 688 ha) were classified as suitable habitat for foraging or reproduction, and approximately one third of these (11 745 ha; 14.3% of all grid cells) met the more stringent requirements of habitat suitable for nesting. Assuming that the loss in native vegetation resulting from urban growth was distributed across habitat types in proportion to their occurrence, suitable habitat for owl nests and territories also would be reduced by 1.2% over the 40-year period. This loss rate translated to a loss of 404 ha of suitable habitat, of which 141 ha were suitable for reproduction.

Areas with sufficient suitable nesting habitat within 200 ha to support a nest stand were associated with only 4.2% of the sample units, indicating that the spatial distribution of nesting habitat was not optimal and that suitable nest stands were limited in the basin. We found that the percent of sample units able to support a nest stand was further lowered when we considered reductions in the availability of suitable habitat resulting from existing development (Table 2). When we applied the development threshold, the figure dropped only slightly to 3.1%, representing only 73.8% of suitable nest stands remaining available (a loss of 26.2%). Eliminating suitable habitat with intrusions of development resulted in a greater drop to 2.9%, leaving 69.0% of suitable nest stands available. When both habitat reductions were applied, sample units meeting the habitat requirements dropped to 2.3%, representing a reduction in suitable nest stands of nearly 50%. Future urban development resulted in only a 10% loss of suitable nest stands based on habitat alone compared to the potential losses of 25–50% resulting from the presence of current development (Table 2).

Areas with sufficient suitable habitat within 1000 ha to support a territory were associated with nearly half (48.3%) of the sample units. When the development threshold was applied, the amount of suitable habitat dropped to 34.9%, representing only 72.3% of suitable territories remaining available (a loss of 27.7%). A similar magnitude reduction resulted from eliminating suitable habitat

Table 2
Reductions in available suitable habitat for the California spotted owl (*Strix occidentalis occidentalis*) at nest stand and territory scales resulting from current and future urban development. Limits on availability of suitable habitat were based on maximum development tolerated throughout the use area (development threshold; 5% for nest stands and 10% for territories) and imbedded in suitable habitat (development intrusion; <1%) were applied to the current landscape and the landscape after 40 years of urban growth.

Scenario	Limits on habitat availability	Nest stands		Territories	
		Qualifying units (%)	Available (%)	Qualifying units (%)	Available (%)
Current	None*	4.2	100.0	48.3	100.0
Current	Development threshold limit	3.1	73.8	34.9	72.3
	Development intrusion limit	2.9	69.0	35.8	74.1
	Threshold and intrusion limits	2.3	54.8	30.1	62.3
Future	None	3.8	90.5	46.3	95.9
	Development threshold limit	2.5	59.5	28.8	59.6
	Development intrusion limit	2.5	59.5	33.1	68.5
	Threshold and intrusion limits	1.8	42.9	25.9	53.6

* All suitable habitat available.

grid cells containing ≥1% development, leaving 74.1% of suitable territories remaining. When both habitat reductions were applied, sample units meeting the criteria dropped to 30.1%, representing a loss of over one third of suitable territories. Future urban development resulted in <5% loss of suitable territories based on habitat alone compared to the estimated losses of 25–40% resulting from the presence of current development (Table 2).

4. Discussion

We derived a fine-grained data layer that depicted a continuum of urban land development across a large landscape. The approach offers a versatile urban land development gradient that has many applications, including the assessment of relationships between development and habitat suitability, species distribution, and biological diversity. Spatially comprehensive land-use data are available for many urbanizing areas, and the straightforward method we used could be replicated elsewhere to evaluate the current and potential future impacts of land development with a high level of spatial specificity. Our development modeling approach avoided many of the identified shortcomings associated with categorical approaches to characterizing urban land development namely the classification of types by levels of development, the delineation of boundary types, and limitations in the spatial resolution at which development can be depicted. Although the depiction of urban land development as a gradient is not new (McDonnell and Pickett, 1990; Luck and Wu, 2002), our approach was uniquely effective in an area of intricate urban–wildland interface where other gradient metrics, such as distance from the urban core, would have been likely to perform poorly (Alberti et al., 2001). Because our approach avoids pre-stratifying the landscape by species- or application-specific criteria, the resulting urban gradient can be used to evaluate the potential effects of urbanization on a myriad of species and other ecosystem elements with different relevant spatial scales, types of sensitivities, and threshold levels of alteration.

Our habitat assessment example demonstrated that the portrayal of development as a continuum is important in the study of landscapes where development is highly interspersed with native vegetation. Exurban landscapes typically exhibit some level of interspersion between human development and wildlands, while a significant portion of land area may remain as native ecosystems (Odell and Knight, 2001). We found that the potential overestimate in available habitat for the California spotted owl resulting from intrusions of development was greater than the reduction in available habitat caused by 40 years of growth in the urban environment. This magnitude of error could have important implications for evaluating population persistence in current or future landscapes for species with sensitivities to human disturbance and fine-scale habitat fragmentation.

Perhaps the greatest advantage of our development model is the ability to seamlessly depict development at a high resolution across large landscapes, which confers both spatial and temporal contiguity. Many studies of urban ecosystems create interpretations of development within circumscribed study areas to address relatively narrow, short-term research questions (e.g., Blair, 1996; Germaine and Wakeling, 2001; Miller et al., 2003; Crooks et al., 2004). These approaches, although individually robust, fall short of building temporally and spatially contiguous knowledge bases that can be used to address multiple research and management questions over time (e.g., Berling-Wolff and Wu, 2004a,b). Ideally, a full-landscape development surface enables the creation of spatially and temporally contiguous predictions across current and future landscapes about the fate of populations (e.g., probability of occurrence, abundance, reproductive success), and/or suitable habitat (e.g., habitat quantity, quality, and spatial distribution) for multiple species. Future landscape conditions can be modeled using a number of techniques (Berling-Wolff and Wu, 2004a), or the development model can be refreshed at points in time to provide a retrospective look at landscape change. Of course retrospective analyses would also require an update of modeling assumptions, given that attributes of land-use types may change over time.

In our landscape, the simplifying assumptions we used to assign development to pixels did not result in any substantive loss of information, as evidenced by the close correspondence between modeled development values and the photo-interpreted development values. Similarly constructed parcel-based development models could include additional considerations and attributes that would make the model even more robust and discriminating. For example, we did not differentiate the relative impacts of different land-use types, although these impacts on species and their habitats can differ greatly (Dunford and Freemark, 2005). Some investigators have quantified the relative ecological value or degradation associated with various land uses (e.g., Brown and Vivas, 2005), while others have ranked the relative emerits of buildings, vegetation, and ground cover as habitat for various species (Cadenasso et al., 2007). Further, the use of average development values and their random allocation within sample units was computationally expeditious, but variation in the levels of development within and among land-use types could be preserved by allocating development levels according to the distribution of values in the sample of parcels from each land-use type. Finally, the spatial allocation of development to

3 m × 3 m pixels within parcels could be programmed to mimic existing patterns of development in the landscape, and future growth rates and locations could be modeled to account for market forces under various potential social and economic conditions.

In conclusion, land-use planners shoulder a tremendous responsibility in determining the fate of local and regional biological diversity in urbanizing landscapes by shaping the extent and character of the urban footprint (Perlman and Milder, 2005; Theobald et al., 2005). Given the substantial ecological consequences of landscape design, readily accessible, easily interpreted, and versatile analytic tools are necessary to aid the assessment of ecological consequences of different development options available to planners and regulators.

Acknowledgements

The development model was created to support a study of the effects of urbanization on biological diversity—the entire research team shaped the model, including Dennis Murphy, Kirsten Heckmann, Monte Sanford, Susan Merideth, and Marcel Holyoak. Funding was provided by the U.S. Forest Service Lake Tahoe Basin Management Unit, Tahoe Regional Planning Agency (TRPA), Nevada Division of State Lands, and the Southern Nevada Public Lands Management Act. Thanks to Gary Weigel and Jim Brockett at TRPA for their help with permitting information, John Keane for his support, and to all reviewers, including Debbie Elliott-Fisk and Peter Stine, for their insightful comments.

Appendix A. Land-use types in the Lake Tahoe basin used to build a GIS model of urban development. N/A = not available

Land-use type	Average percent developed	Standard error	Number of parcels	Total area (ha)
Summer home	14	6	519	95
Domestic animal raising	20	N/A	1	10
Developed campgrounds	22	15	12	353
Abandoned residential structure	30	42	2	<1
Cultural facilities	30	26	6	39
Laundries and dry-cleaning plant	35	49	2	<1
Transmission and receiving facilities	36	5	5	2
Outdoor recreation concessions	48	35	4	3
Participant sports facilities	49	39	8	17
Accessory use to a single-family dwelling	50	16	319	<1
Pipelines and power transmissions	50	36	3	41
Single-family dwelling	51	20	28 032	3535
Cemeteries	52	28	5	5
Animal husbandry services	53	29	4	1
Bed and breakfast	53	6	3	25
Churches	53	23	33	1
Beach recreation	54	27	69	65
Group facilities	54	26	7	103
Public utility centers	54	25	112	37
Undeveloped campgrounds	60	N/A	1	2
Recreation centers	61	23	12	21
Health care services	63	15	37	8
School – college	64	34	8	61
Local Public health and safety facilities	65	28	44	43
Government offices	66	23	19	29
Hospitals	67	15	3	7
Condominium common area	68	27	512	422
Nursery	68	29	6	52
Outdoor retail sales	69	27	8	1
Boat launching facilities	70	27	7	1
Day-use areas	70	24	43	1
Printing and publishing	70	30	3	1
Residential care	70	N/A	1	9
Social service organizations	70	41	3	110
Visitor information centers	70	22	4	1
Eating and drinking places	72	21	110	1
Personal services	73	32	31	5
Mobile home park	75	28	42	39
Post office	76	29	10	41
Regional public health and safety facilities	76	32	17	4
Multiple family dwelling (2–4 units)	77	21	1720	9
Multiple family dwelling (5–10 units)	77	24	206	2
Power generating	77	23	7	204
Golf courses	78	16	45	35
Local assembly and entertainment	78	26	8	3
School – Kindergarten through secondary	78	19	24	140
Downhill ski facilities	79	20	45	397
Nursing and personal care	80	20	2	43
Rural sports	80	N/A	1	2
Transit stations and terminals	80	0	2	5
Storage yards	81	22	28	<1

Appendix A (*Continued*)

Land-use type	Average percent developed	Standard error	Number of parcels	Total area (ha)
Day care/pre-school	82	21	12	29
Fuel and ice dealers	82	25	5	17
Hotel/motel	82	24	255	2
Vehicle storage and parking	82	23	70	2
Amusements and recreation services	83	14	7	97
Contract construction services	83	12	26	4
Broadcasting studios	85	7	2	14
Food and beverage retail sales	87	22	24	1
Professional offices	87	22	189	39
Multiple family dwelling (10+ units)	88	22	75	28
Gaming: non-restricted	88	28	10	7
Vehicle and freight terminals	89	18	8	30
Business support services	90	0	2	4
Furniture, home furnishings and equipment	90	14	9	1
General merchandise stores	90	17	178	8
Sales lots	90	N/A	1	13
Schools – business and vocational	90	N/A	1	<1
Small scale manufacturing	90	16	23	<1
Industrial services	91	15	21	<1
Auto repair services	92	14	55	6
Service Stations	92	15	35	25
Repair services	93	8	6	1
Time sharing (hotel/motel design)	93	10	8	12
Abandoned commercial structure	94	15	7	6
Auto dealers	94	14	8	1
Food and kindred products	94	17	27	<1
Wholesale and distribution	94	9	5	2
Financial services	96	7	17	1
Warehousing	96	15	200	31
Airfields	100	N/A	1	16
Batch plants	100	0	5	5
Building materials and hardware	100	0	18	13
Condominium	100	0	7239	90
Mobile home dwelling	100	0	727	1
Marinas	100	0	178	3
Privately-owned assembly	100	0	2	29
Recycling and scrap	100	0	6	<1
Secondary storage	100	N/A	1	4
Time sharing (residential design)	100	0	141	2

References

Alberti, M., Botsford, E., Cohen, A., 2001. Quantifying the urban gradient: linking urban planning to ecology. In: Marzluff, J.M., Bowman, R., Donelly, R. (Eds.), Avian Ecology and Conservation in an Urbanizing World. Kluwer Academic Publishers, Boston, MA, pp. 89–115.

Berling-Wolff, S., Wu, J., 2004a. Modeling urban landscape dynamics: a review. Ecol. Res. 19, 119–129.

Berling-Wolff, S., Wu, J., 2004b. Modeling urban landscape dynamics: a case study in Phoenix, USA. Urban Ecosyst. 7, 215–240.

Blair, R.B., 1996. Land use and avian species diversity along an urban gradient. Ecol. Appl. 6, 506–519.

Blumstein, D.T., Fernandez-Juricic, E., Zollner, P.A., Garity, S.C., 2005. Inter-specific variation in avian responses to human disturbance. J. Appl. Ecol. 42, 943–953.

Boyle, S.A., Samson, F.B., 1985. Effects of nonconsumptive recreation on wildlife: a review. Wildl. Soc. Bull. 13, 110–116.

Brown, M.T., Vivas, B., 2005. Landscape development intensity index. Environ. Monit. Assess. 101, 289–309.

Cadenasso, M.L., Pickett, S.T.A., Schwarz, K., 2007. Spatial heterogeneity in urban ecosystems: reconceptualizing land cover and a framework for classification. Front. Ecol. Environ. 5, 80–88.

Cahill, K., Whitley, M.G., Villanueva, G., Bencke, N., 2002. LTBMU transportation. USDA Forest Service, South Lake Tahoe, CA.

California Department of Fish and Game, c., 2002. California Wildlife Habitat Relationships Program Database, Version 8.0. Sacramento, CA.

California Department of Transportation, 2001. Highway Design Manual. Sacramento, CA.

California State Parks, 2000. State Parks Roads and Trails, Sacramento, CA.

Call, D.R., 1990. Home range and habitat use by California spotted owls in the central Sierra Nevada. Masters thesis, Humboldt State University, Arcata, CA.

Churcher, P.B., Lawton, J.H., 1987. Predation by domestic cats in an English UK village. J. Zool. (Lond.) 212, 439–456.

Crooks, K.R., Suarez, A.V., Bolger, D.T., 2004. Avian assemblages along a gradient of urbanization in a highly fragmented landscape. Biol. Conserv. 115, 451–462.

Dobrowski, S.Z., Greenberg, J.A., Ustin, S.L., 2005. Tahoe Basin Existing Vegetation Map v. 4.1, http://casil.ucdavis.edu/projects/tbevm, Davis, CA.

Dunford, W., Freemark, K., 2005. Matrix matters: effects of surrounding land uses on forest birds near Ottawa, Canada. Landsc. Ecol. 20, 497–511.

ESRI Inc., 2004. ArcMap Version 9. 0. Environmental Systems Research Institute, Redlands, CA.

Forman, R.T.T., Reineking, B., Hersperger, A.M., 2002. Road traffic and nearby grassland bird patterns in a suburbanizing landscape. Environ. Manage. 29, 782–800.

Germaine, S.S., Wakeling, B.F., 2001. Lizard species distributions and habitat occupation along an urban gradient in Tucson, Arizona, USA. Biol. Conserv. 97, 229–237.

Gutierrez, R.J., Verner, J., McKelvey, K.S., Noon, B.R., Steger, G.N., Call, D.R., LaHaye, W.S., Bringham, B.B., Senser, J.S., 1992. Habitat relations of the California spotted owl. In: Verner, J., McKelvey, K.S., Noon, B.R., Gutierrez, R.J., Gould, G.I.J., Beck, T.W. (Eds.), The California Spotted Owl: A Technical Assessment of its Current Status. Gen. Tech. Rep. PSW-GTR-133, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.

Heyer, W.R., Donnelly, M.A., McDiarmid, R.W., Hayek, L.C., Foster, M.S. (Eds.), 1994. Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians. Smithsonian Institution Press, Washington, DC.

Homer, C., Dewitz, J., Fry, J., Coan, M., Hossain, N., Larson, C., Herold, N., McKerrow, A., VanDriel, J.N., Wickham, J., 2007. Completion of the 2001 National Land Cover Database for the conterminous United States. Photogrammetr. Eng. Remote Sens. 73, 337–341.

Hunsaker, C.T., Boroski, B.B., Steger, G.N., 2002. Relations between canopy cover and the occurrence and productivity of California spotted owls. In: Scott, M.J., Heglund, P.J., Morrison, M.L., Haufler, J.B., Raphael, M.G., Wall, W.A., Samson, F.B. (Eds.), Predicting Species Occurrences – Issues of Accuracy and Scale. Island Press, Washington, DC, pp. 687–700.

Knight, R.L., Gutzwiller, K.J., 1995. Wildlife and Recreationists: Coexistence through Management and Research. Island Press, Washington, DC.

Kosis, S.M., English, D.B.K., Zarnoch, S.J., Arnold, R.S., Warren, L., 2002. National visitor use monitoring results. Pacific Southwest Region, USDA Forest Service, Vallejo, CA. http://www.fs.fed.us/recreation/programs/nvum/reports/year5/kaibab.doc.

Laymon, S.A., 1988. Ecology of the spotted owl in the central Sierra Nevada. Unpublished dissertation. University of California, Berkeley, CA.

Luck, M., Wu, J.G., 2002. A gradient analysis of urban landscape pattern: a case study from the Phoenix metropolitan region, Arizona, USA. Landsc. Ecol. 17, 327–339.

Manley, P.N., Fites-Kaufman, J.A., Barbour, M.G., Schlesinger, M.D., Rizzo, D.M., 2000. Biological integrity. In: Murphy, D.D., Knopp, C.M. (Eds.), Lake Tahoe Watershed Assessment, vol. I. Gen. Tech. Rep. PSW-GTR-175. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA, pp. 401–598.

Manley, P.N., Murphy, D.D., Campbell, L.A., Heckmann, K.E., Merideth, S., Parks, S.A., Sanford, M.P., Schlesinger, M.D., 2006. Biotic diversity interfaces with urbanization in the Lake Tahoe basin. Calif. Agric. 60, 59–64.

Marzluff, J.M., Ewing, K., 2001. Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. Restor. Ecol. 9, 208–292.

Marzluff, J.M., Bowman, R., Donnelly, R.E., 2001. A historical perspective on urban bird research: trends, terms and approaches. In: Marzluff, J.M., Bowman, R., Donnelly, R.E. (Eds.), Avian Conservation and Ecology in an Urbanizing World. Kluwer Academic, New York, pp. 1–15.

Mayer, K.E., Laudenslayer, W.F., 1988. A Guide to Wildlife Habitats of California. State of California, Resources Agency, Department of Fish and Game, Sacramento.

McDonnell, M.J., Pickett, S.T.A., 1990. Ecosystem structure and function along urban rural gradients—an unexploited opportunity for ecology. Ecology 71, 1232–1237.

McKinney, M.L., 2002. Urbanization, biodiversity, and conservation. Bioscience 52, 883–890.

McKinney, M.L., 2006. Urbanization as a major cause of biotic homogenization. Biol. Conserv. 127, 247–260.

Miller, J.R., Wiens, J.A., Hobbs, N.T., Theobald, D.M., 2003. Effects of human settlement on bird communities in lowland riparian areas of Colorado (USA). Ecol. Appl. 13, 1041–1059.

Nechodom, M., Rountree, R., Dennis, N., Robison, H., Goldstein, J., 2000. Social, economic, and institutional assessment. In: Murphy, D.D., Knopp, C.M. (Eds.), Lake Tahoe Watershed Assessment, vol. I. Gen. Tech. Rep. PSW-GTR-175. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA, pp. 601–687.

Nevada Division of State Parks, c., 2000. Roads and trails: Lake Tahoe-Nevada State Park, Carson City, NV.

Odell, E.A., Knight, R.L., 2001. Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. Conserv. Biol. 15, 1143–1150.

Perlman, D.L., Milder, J.C., 2005. Practical Ecology: For Planners, Developers, and Citizens. Island Press, Washington, DC.

Ralph, C.J., Guepel, G.R., Pyle, P., Martin, T.E., DeSante, D.F., 1993. Handbook of Field Methods for Monitoring Landbirds. Gen. Tech. Rep. PSW-GTR-144. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.

Sandström, U.G., Angelstam, P., Khakee, A., 2006. Urban comprehensive planning—identifying barriers for the maintenance of functional habitat networks. Landsc. Urban Plan. 75, 43–57.

SAS Institute Inc., 2000. JMP Version 6.0. SAS Institute Inc., 100 SAS Campus Drive, Cary, NC, 27513-2414.

Tahoe Regional Planning Agency, 2001. Parcel-based Land Use. Stateline, NV.

Theobald, D.M., 2004. Placing exurban land-use change in a human modification framework. Front. Ecol. Environ. 2, 139–144.

Theobald, D.M., Spies, T., Kline, J., Maxwell, B., Hobbs, N.T., Dale, V.H., 2005. Ecological support for rural land use. Ecol. Appl. 15, 1906–1914.

Turner, M.G., 1989. Landscape ecology: the effect of pattern on process. Ann. Rev. Ecol. Syst. 20, 171–197.

Turner, M.G., Gardner, R.H., O'Neill, R.V., 2001. Applied landscape ecology. In: Turner, M.G., Gardner, R.H., O'Neill, R.V. (Eds.), Landscape Ecology in Theory and Practice. Springer-Verlag, New York, NY, pp. 289–325.

USDA Forest Service, 2004. Sierra Nevada forest plan amendment, final supplemental environmental impact statement, record of decision. Vallejo, CA. http://www.fs.fed.us/r5/snfpa/final-seis/.

Verner, J., McKelvey, K.S., Noon, B.R., Gutierrez, R.J., Gould, G.I.J. (Eds.), 1992. The California Spotted Owl: A Technical Assessment of its Current Status. Gen. Tech. Rep. PSW-GTR-133, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.

Wear, D.N., Turner, M.G., Naiman, R.J., 1998. Land cover along an urban–rural gradient: implications for water quality. Ecol. Appl. 8, 619–630.

Wickham, J., Norton, D.J., 1994. Mapping and analyzing landscapes. Landsc. Ecol. 9, 7–23.

Wilson, D.E., Cole, F.R., Nichols, J.D., Rudran, R., Foster, M.S. (Eds.), 1996. Measuring and Monitoring Biological Diversity: Standard Methods for Mammals. Smithsonian Institute Press, Washington, DC.

Zielinski, W.J., Kucera, T.E. (Eds.), 1995. A Detection Manual for Wolverine, Fisher, Lynx and Marten in the Western United States. USDA Forest Service Gen. Tech. Rep. GTR-PSW-157, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.